INTERSPECIFIC OLFACTORY COMMUNICATION IN THE SOUTHERN PINE BARK BEETLE GUILD[1]

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INTRODUCTION

The southern pine bark beetle guild consists of many species, the most economically significant of which are the five scolytid species, *Dendroctonus frontalis* Zimmermann, *D. terebrans* (Olivier), *Ips calligraphus* (Germar), *I. avulsus* (Eichhoff), and *I. grandicollis* (Eichhoff). All five species co-exist in pine forests across the southern and southeastern United States. When the species cohabit in the same host tree each usually occupies a distinct niche. However, the area occupied by one species generally overlaps with that occupied by another (Fig. 1) (Birch and Svihra 1979, Dixon and Payne 1979, Birch et al. 1980, Svihra et al. 1980, Paine et al. 1981, Wagner et al. 1985.

Host selection, aggregation and colonization by all the various species involves a complex chemical communication system composed of compounds produced both by the beetles and by the host tree. Electrophysiological investigations have shown that each species has antennal olfactory receptors capable of detecting semiochemicals produced by itself and by the other species in the guild (Payne 1970, 1971, 1974, 1975, Payne and Dickens 1976, Dickens and Payne 1977, Payne et al. 1982, 1987, 1988, Smith et al. 1988). Behavioral investigations of some of the species have shown that they respond to intra- and interspecific semiochemicals, as well as to volatiles from beetle-infested host materials (Renwick and Vité 1969, Werner 1972, Hedden et al. 1976, Payne et al. 1978, Richerson and Payne 1979, Dixon and Payne 1980, Billings 1985, Siegfried et al. 1986, Payne et al. 1987, Payne et al. 1988, and Phillips et al. 1989). Investigations have also shown the response patterns of the species to

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trees or logs containing the various members of the guild (Vité et al. 1964, Godbee and Franklin 1976, Birch et al. 1980, Svihra et al. 1980, Svihra 1982, Phillips et al. 1989). In this paper, using both new findings and previously published information, we survey the interspecific olfactory receptor sensitivity of the species for specific pheromones and explore the behavioral responses of the most significant species in the southern pine bark beetle guild to the pheromonal blends of the species.

EXPERIMENTAL METHODS

Antennal olfactory responses were measured using the electroantennogram (EAG) and single-cell techniques (Schneider 1957; Boeckh 1962, Payne 1975, Dickens and Payne 1977). EAGs were recorded with glass capillary, Ag-AgCl microelectrodes filled with 3M KCl. The recording electrode was inserted in the antennal club, and the indifferent electrode was inserted in the beetle's head capsule or mouth. Single-cell recordings (SCR) were made using tungsten electrodes with electrolytically polished tips of < 2 u. The recording electrode was inserted at the base of a sensillum in the sensory bands of the antenna; the indifferent electrode was inserted in the mouth. Responses were recorded on magnetic tape and polaroid film. The compounds tested, their source, and their purity are given in Table 1. Test stimuli were delivered as 5 ul aliquots onto a piece of filter paper in a glass cartridge via a 1 L/min airflow. Serial dilutions of the stimuli were presented in order from the lowest to the highest concentration. Dosage-response curves plotted from mean responses to each stimuli were used to determine the relative sensitivity of the olfactory receptors to each compound. The threshold of response, the minimal stimulus concentration at which an EAG was detectable above background, was considered an indication of olfactory receptor sensitivity to a compound.

Table 1. Beetle- and host-tree-produced compounds tested

Compound	Source of supply	Purity (%)
Frontalin		
(+,-)	Chem. Samp. Co.	99
(+)	K. Mori	98
(-)	K. Mori	98
Verbenone		
(+,-)	Chem. Samp. Co.	98
(+)	Chem. Samp. Co.	98
(-)	Chem. Samp. Co.	98
endo-brevicomin	Chem. Samp. Co.	99
Ipsdienol	Borregaard Industries	81
Ipsenol	Borregaard Industries	89
cis-verbenol	Borregaard Industries	95
trans-verbenol	Borregaard Industries	95
α-pinene	Aldrich Chem. Co.	97

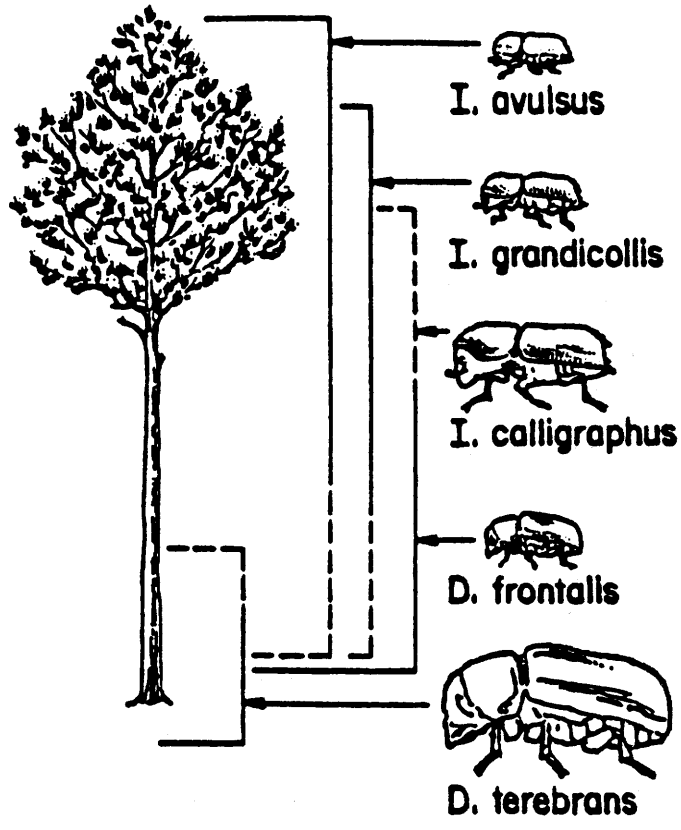

Figure 1. Primary species of the southern pine bark beetle guild and their generalized spatial distribution on the host tree. (From Flamm et al. 1988.)

Our field studies were conducted in the east Texas pine forest during the summer of 1987. To minimize possible effects of host tree odors on beetle response, the studies were carried out in a 2-year-old clear-cut. The surrounding forest was mostly loblolly pine, *Pinus taeda*, and, to the best of our knowledge, no bark beetle infestations were present within ca. a 50-mile radius. At the time, beetle populations in Texas were considered to be at an endemic level. As a result, the number of beetles trapped during the study was low.

Test Compounds

Pheromonal blends for the guild members were determined from published and unpublished reports of pheromone production and were individually formulated and tested. In addition, specific enantiomers of the major pheromonal components were evaluated for *D. frontalis* and the *Ips* spp., since previous research had demonstrated differential production and/or responsiveness based on enantiomeric composition (see references, Table 2). To determine the presence and relative abundance of flying beetles of each species in the test area, a *Dendroctonus* standard composed of frontalin and turpentine and an *Ips* standard composed of ipsdienol, ipsenol, and *cis*-verbenol (Billings 1985) were included as separate treatments in the experiments. A trap baited only with turpentine and a blank trap were included as controls for response to host odor and trap configuration, respectively.

Table 2. Beetle-produced pheromonal blends tested

Species	[1] Sex	[2] Chemical compounds	Compound ratios	Elution rate (mg/24 h)	[3] Reference
D. frontalis	F	(-)-F:(+)-F:TV:V	21.25:3.75:750:6	0.85:0.15:30:0.24	1,2
D. frontalis	M	(+)-ENB:(-)-ENB:EXB:V:TV	0.94:0.03:0.03:800:9	0.94:0.03:L0.03:800:9	2,3
D. terebrans	F	F:TV:V	1:500:50	1:500:50	2,4
	M	EXB:TV:V	1:15:1.1	1:15:1.1	2,4
I. calligraphus	M	(R)-(-)-,(S)-(+)-IPSD:TV:CV	2:2.5:1	0.2:0.25:0.1	5,6
	M	(R)-(-)-IPSD:TV:CV	2:2.5:1	0.2:0.25:0.1	6
	M	(S)-(+)-IPSD:TV:CV	2:2.5:1	0.2:0.25:0.1	6
I. calligraphus	F	TV:CV	5.5:1	4.4:0.8	5
I. avulsus	M	(R)-(-)-,(S)-(+)-IPSD:TV:CV	45:1:1	0.2:0.0044	5,6
	M	(R)-(-)-IPSD:TV:CV	45:1:1	0.2:0.0044	6
	M	(S)-(+)-IPSD:TV:CV	45:1:1	0.2:0.0044	6
I. grandicollis	M	(S)-(-)-,(R)-(+)-IPSE:TV:CV	73:1:1	0.2:0.0027:0.0027	5,7
		(S)-(-)-IPSE:TV:CV	73:1:1	0.2:0.0027:0.0027	7
		(R)-(+)-IPSE:TV:CV	73:1:1	0.2:0.0027:0.0027	7

[1] Sex: F = female; M = male.

[2] CV = *cis*-verbenol, ENB = *endo*-brevicomin, EXB = *exo*-brevicomin, F = frontalin, IPSD = ipsdienol, IPSE = ipsenol, TV = *trans*-verbenol, and V = verbenone.

[3] 1) Stewart et al. 1977, 2) Payne, West, Silverstein (unpubl.), 3) Redlich et al. 1987, 4) Payne et al. 1987, 5) Vité et al. 1972, 6) Vité et al. 1978, and 7) Vité et al. 1976.

Elution Devices and Rates

Based on weight loss/24 h, elution devices were developed and rates determined for each compound tested (Table 2). Glass capillaries and vials of various sizes provided the desired elution rates.

Experimental Design

The multiple funnel trap was used to monitor the beetles' response to the different pheromonal blends (Lindgren 1983). Traps were placed ca. 45 m apart in a single, straight row running through the center of the clear-cut. Initially, treatments were assigned positions randomly. Thereafter, treatments were advanced one position each subsequent day in order to minimize positional effects and disproportionate trap catches caused by any nonrandom distribution of beetles. Thus each treatment occupied each position during the 20-day experiment. Every 24 h, trapped beetles were removed and placed in labeled vials for subsequent counting and sexing. Chi Square and/or Fisher's exact tests were used to analyze the data, followed by a binomial test for paired comparisons, when appropriate (Sokal and Rohlf 1981).

RESULTS AND DISCUSSION

Olfactory Perception

Electroantennogram analyses of the species have consistently shown that each species possesses more receptors with lower thresholds for compounds produced by conspecifics and to which they are behaviorally most responsive (Payne 1970, 1971, 1974, Dickens and Payne 1977, Payne et al. 1982, 1988, Smith et al. 1988). For examples, see Figs. 2 and 3.

More detailed investigations of the peripheral olfactory receptor systems have been made using single cell recording (SCR) techniques (Fig. 4).

Both general and chiral-specific acceptors have been identified, as well as a wide variety of olfactory cell types with different degrees of receptor specificities which range along a continuum from cells narrowly tuned to a single compound to cells broadly tuned to a number of different compounds (Figs. 5-7).

Compounds which attract and/or arrest, enhance attraction or reduce attraction, may be perceived by a common neuron and acceptor. These overlapping acceptor specificities may provide the beetles with the genetic plasticity needed to code both qualitative and quantitative information about several behaviorally significant odors present in the insects' environment.

Behavioral Response

The responses of *D. frontalis*, *D. terebrans*, *I. calligraphus*, *I. avulsus*, and *I. grandicollis* to the *Dendroctonus* and *Ips* standards (treatments 17 and 18) verified that the species were present throughout the test area for the duration of the experiment, even though, due to their endemic population levels, the number of beetles trapped was low.

D. frontalis

As expected, both male and female *D. frontalis* were attracted to the pheromonal blends of female *D. frontalis* and, to a lesser extent, female *D. terebrans* (treatments 1 and 4) (Fig. 8). Attraction to both blends can be attributed to the presence of frontalin and *trans*-verbenol. *D. frontalis* has been

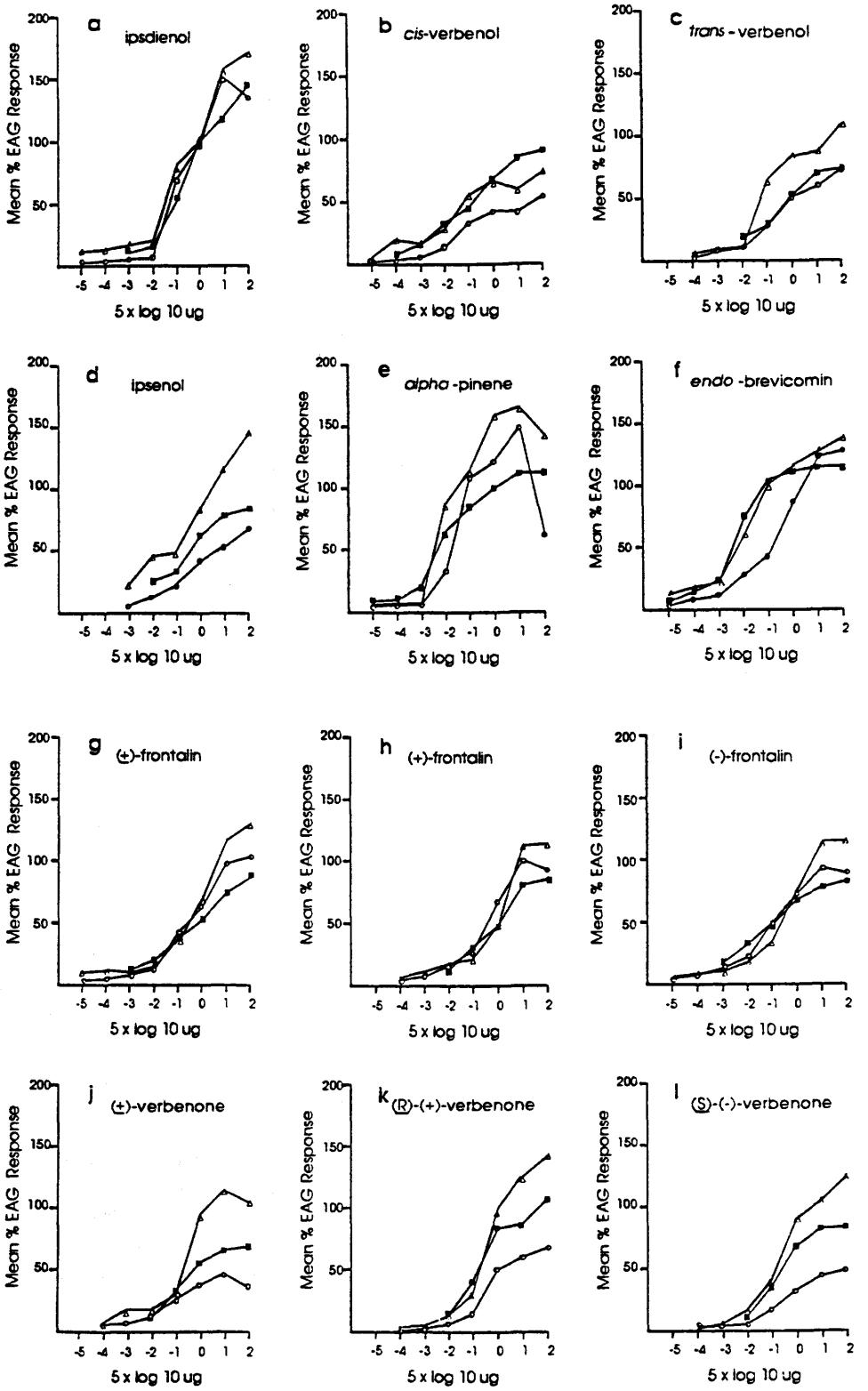

Figure 2. Mean percentage response of *I. avulsus*, *I. calligraphus*, and *I. grandicollis* to behavioral chemicals. Means are percentage of EAG to the standard ipsdienol. ○ = *I. avulsus*; ■ = *I. calligraphus*; Δ = *I. grandicollis*. (From Smith et al. 1988.)

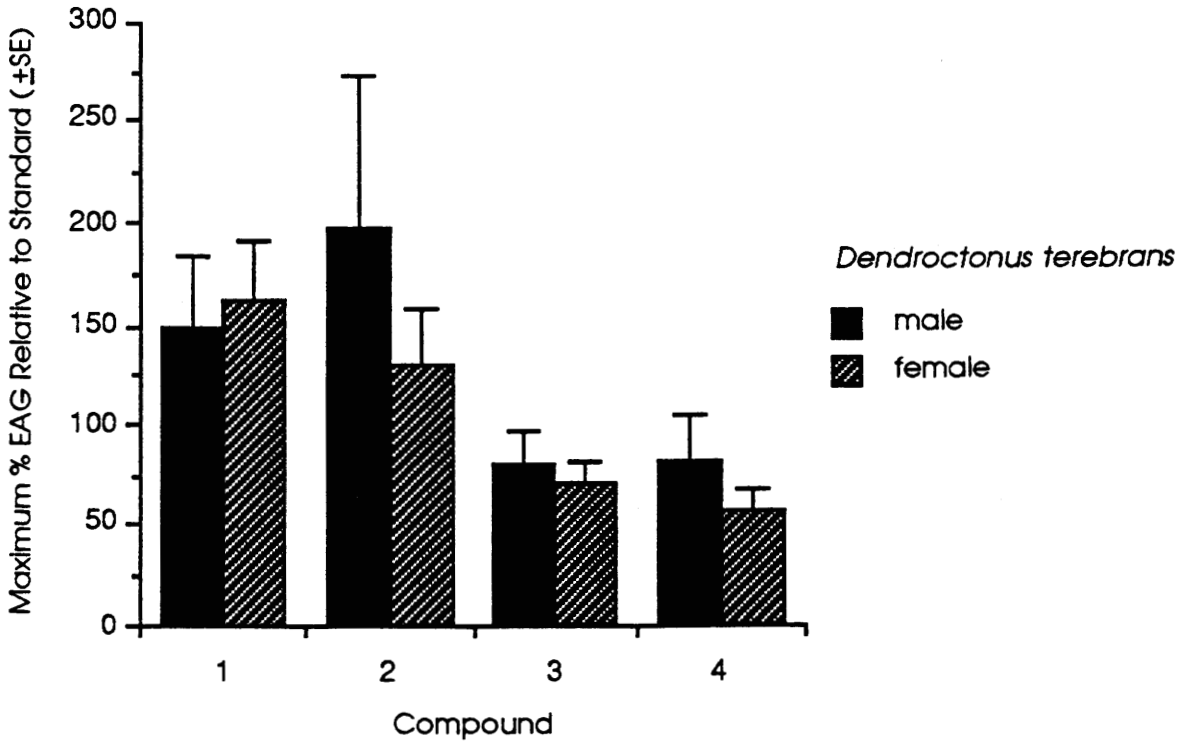

Figure 3. Maximal percentage of EAGs to behavioral chemicals recorded from male and female *Dendroctonus terebrans* N = 5; vertical bars represent ± $\bar{x}$ SE. Standard = 5 ug frontalin. 1 = Frontalin, 2 = *endo*-brevicomin, 3 = *trans*-verbenol, 4 = turpentine. (From Payne et al. 1987.)

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reported to be attracted to frontalin and frontalin plus *trans*-verbenol (Renwick 1969, Renwick and Vité 1969, 1970, Payne et al. 1978, Billings 1985). *Trans*-verbenol has been reported significantly to enhance the attraction of *D. frontalis* to frontalin (Renwick 1969, Renwick and Vité 1970, Payne et al. 1978).

Male and female *D. frontalis* were not attracted to the pheromonal blends of male *D. frontalis* (treatment 2) or male *D. terebrans* (treatment 5). Responses of both sexes of *D. frontalis* to the pheromonal blend of female *D. frontalis* was significantly ($P < 0.05$) reduced by the simultaneous presence of the male *D. frontalis* blend (treatment 3). In part, these results can be attributed to the relatively high proportion of verbenone eluted from the blends of both male *D. frontalis* and male *D. terebrans*. Eluted at relatively high rates, verbenone has been reported to reduce *D. frontalis* attraction to frontalin plus α-pinene and/or *trans*-verbenol and frontalin plus turpentine (Renwick and Vité 1969, Payne et al. 1978). The results can also be attributed to the presence of *exo*-brevicomin, eluted from the blend of male *D. terebrans*, and *exo*-brevicomin plus *endo*-brevicomin, eluted from the blend of male *D. frontalis*. The brevicomins reduce *D. frontalis* attraction to frontalin plus α-pinene (Vité and Renwick 1971a, Payne et al. 1978). *D. frontalis* attraction to frontalin plus turpentine, with and without *trans*-verbenol, has also been reported to be reduced by *endo*-brevicomin (Payne et al. 1978). More specifically, Vité et al. (1985) reported that (-)-*endo*-brevicomin significantly reduced *D. frontalis* attraction to frontalure (1:2 ratio of frontalin and α-pinene) plus turpentine.

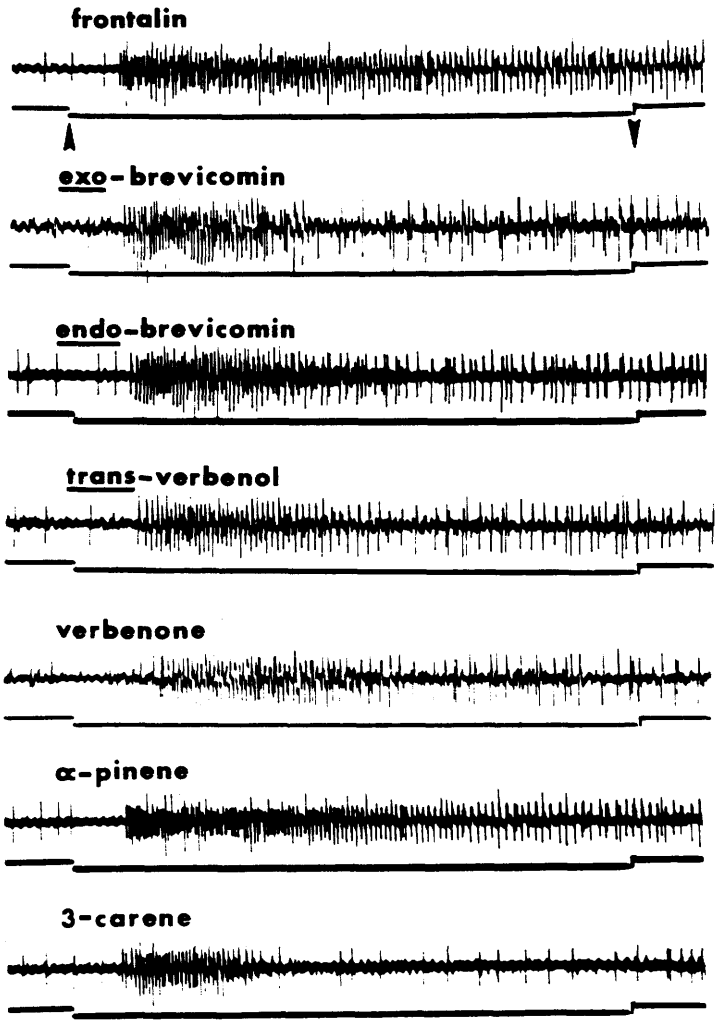

Figure 4. Single-cell response from a sensillum basiconicum of a *D. frontalis* female to pheromones and host tree terpenes. Displaced horizontal bar (indicated by arrows) represents 1 sec stimulation. Delay from stimulus onset to spike initiation was due to an artifact in delivery system. (From Dickens and Payne 1978.)

None of the pheromonal blends of the *Ips* species was attractive to *D. frontalis* (treatments 7-16). The results correspond to the report by Billings (1985) of the lack of attraction of *D. frontalis* to an *Ips* pheromone blend, a mixture of 2 percent *cis*-verbenol, 2 percent ipsenol, and 2 percent ipsdienol in a vaseline-based paste, with and without turpentine. In addition, studies using beetle-infested pine bolts provided no evidence for the attraction of *D. frontalis* to bolts infested with *I. calligraphus*, *I. avulsus*, or *I. grandicollis* (Vité et al. 1964, Birch and Svihra 1979, Birch et al. 1980, Svihra et al. 1980, Svihra 1982).

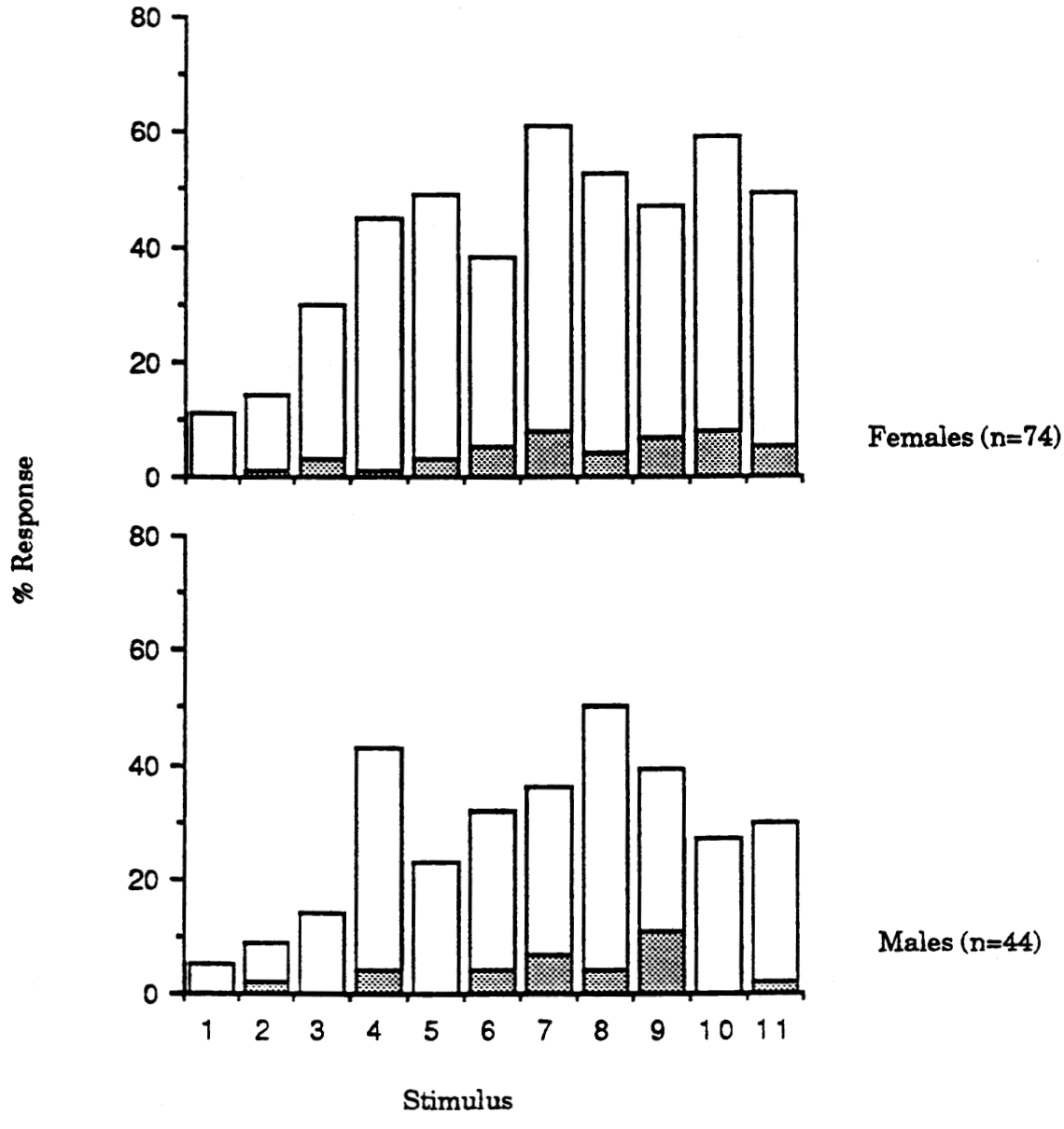

Figure 5. Percentage of *Ips grandicollis* olfactory cells which responded to stimuli. Shaded area equals percentage of cells which responded to only one compound. 1) spontaneous activity, 2) air, 3) pentane, 4) α-pinene, 5) frontalin, 6) *endo*-brevicomin, 7) *trans*-verbenol, 8) *cis*-verbenol, 9) verbenone, 10) ipsdienol, and 11) ipsenol.

D. terebrans

D. terebrans were trapped in such low numbers that analysis of their cross-attraction was not possible (Fig. 9). It should be noted, however, that the lack of response of *D. terebrans* to frontalin, frontalure, and *trans*-verbenol, separately, has been reported (Payne et al. 1987, Phillips et al. 1989). In combination with a high elution rate of turpentine, the pheromones were significantly attractive to

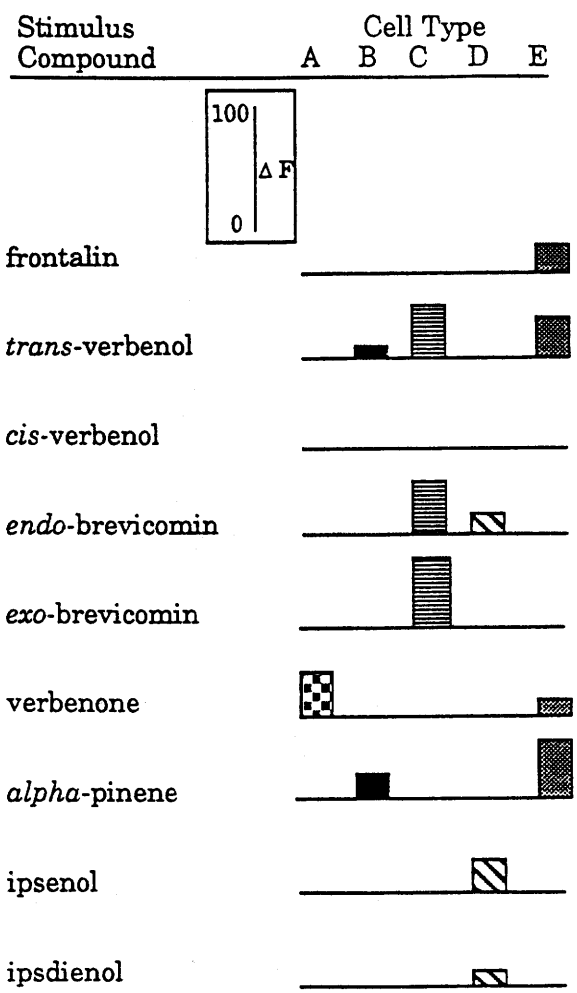

Figure 6. Relative frequency of nerve spikes from *D. frontalis* olfactory cells in response to semiochemicals.

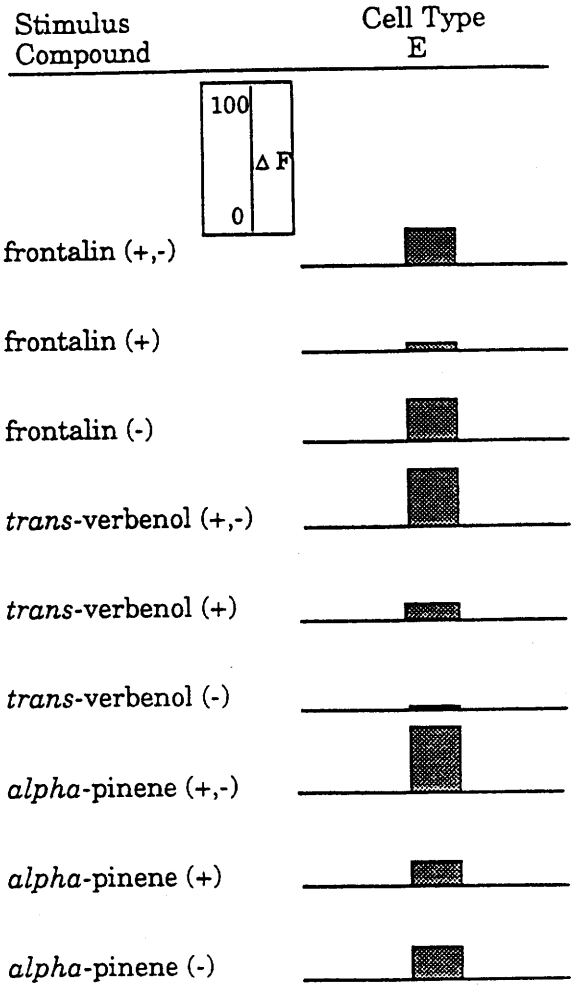

Figure 7. Relative frequency of nerve spikes from a single *D. frontalis* olfactory cell in response to semiochemicals and enantiomers.

D. terebrans, which indicates the presence of pheromonal-based interspecific communication between *D. terebrans* and *D. frontalis*, as reported earlier (Payne et al. 1987).

I. calligraphus

Male and female *I. calligraphus* were attracted to the pheromonal blends of male *I. calligraphus* and *I. avulsus* containing either racemic ipsdienol (treatments 7 and 11) or (R)-(-)-ipsdienol (treatments 8 and 12) (Fig. 10). More *I. calligraphus* ($P > 0.05$) were attracted to the male *I. calligraphus* blend containing racemic ipsdienol (treatment 7) than to the blend containing (R)-(-)-ipsdienol (treatment 8). But *I. calligraphus* were not attracted to the blends of male *I. calligraphus* or male *I. avulsus* containing (S)-(+)-ipsdienol (treatments 9 and 13). Our results agree with earlier reports of the attraction of *I. calligraphus* to ipsdienol plus *cis*-verbenol and ipsdienol plus *trans*-verbenol (Renwick and Vité 1972).

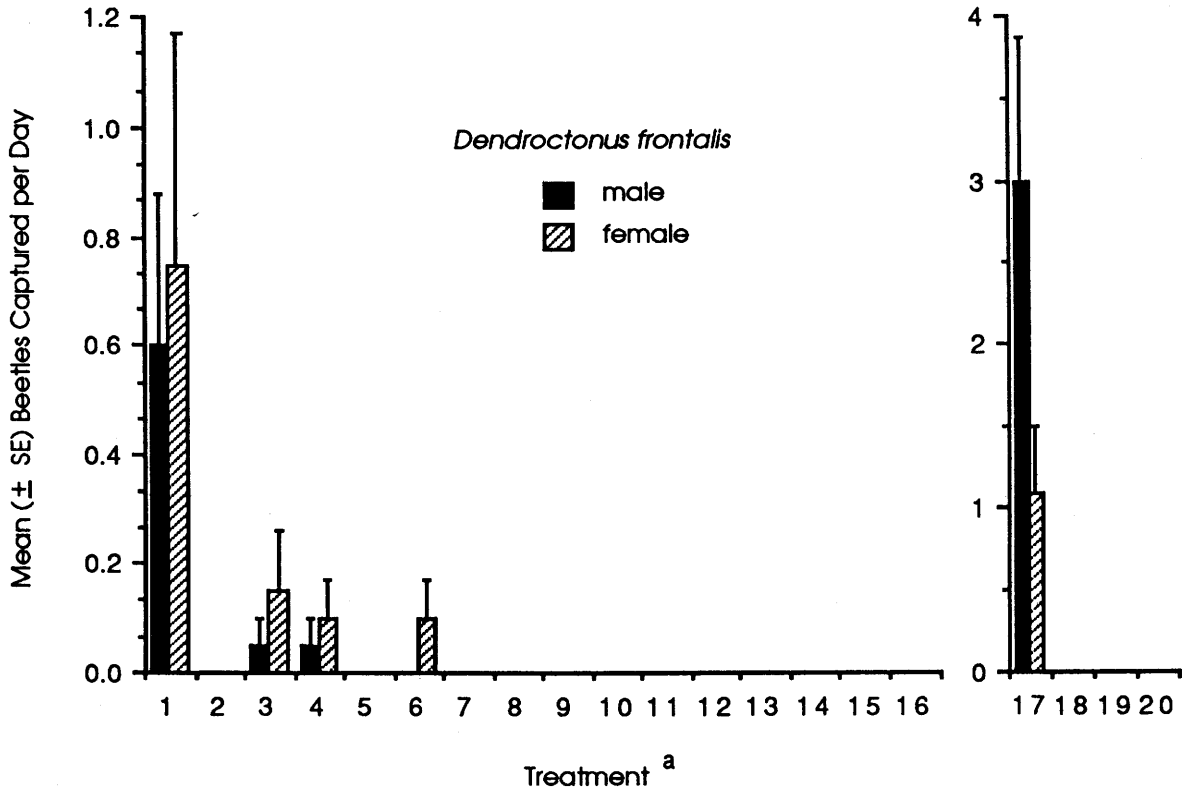

Figure 8. Mean number of *Dendroctonus frontalis* trapped in response to pheromonal compounds eluted at varying rates. [a]See Table 2. Vertical bars represent standard errors of means.
1) (-)-F:(+)-F:TV:V, 2) (+)-ENB:(-)-ENB:EXB:V:TV, 3) 1+2, 4) F:TV:V, 5) EXB:TV:V, 6) 4+5, 7) (R)-(-)-,(S)-(+)-IPSD:TV:CV, 8) (R)-(-)-IPSD:TV:CV, 9) (S)-(+)-IPSD:TV:CV, 10) TV:CV, 11) (R)-(-)-,(S)-(+)-IPSD:TV:CV, 12) (R)-(-)-IPSD:TV:CV, 13) (S)-(+)-IPSD:TV:CV, 14) (S)-(-)-,(R)-(+)-IPSE:TV:CV, 15) (S)-(-)-IPSE:TV:CV, 16) (R)-(+)-IPSE:TV:CV, 17) *Dendroctonus* standard, 18) *Ips* standard, 19) turpentine standard, and 20) unbaited blank trap.

More specifically, the results are in agreement with the report that for *I. calligraphus* (R)-(-)-ipsdienol plus *cis*-verbenol was attractive, whereas (S)-(+)-ipsdienol plus *cis*-verbenol was not (Vité et al. 1978). However, the results reported here are not consistent with the report by Vité et al. (1978) that (S)-(+)-ipsdienol significantly reduced the attraction of *I. calligraphus* to (R)-(-)-ipsdienol plus *cis*-verbenol.

The pheromonal blends of male *I. grandicollis* were not attractive to *I. calligraphus* (treatments 14-16). Although there are no reported analyses of the behavioral response of *I. calligraphus* to the *I. grandicollis* pheromone, ipsenol, when tested alone, the results presented here could be attributed to the lack of attraction of *I. calligraphus* to ipsenol. By contrast, Birch et al. (1980) showed attraction of *I. calligraphus* to *I. grandicollis*-infested bolts; however, other researchers reported the lack of such attraction (Vité et al. 1964, Birch et al. 1980, Svihra 1982).

The *D. frontalis* blends were not attractive to *I. calligraphus*; for *D. terebrans* only the female blend exerted an attraction and that was slight. Dixon and Payne (1980) also reported the lack of

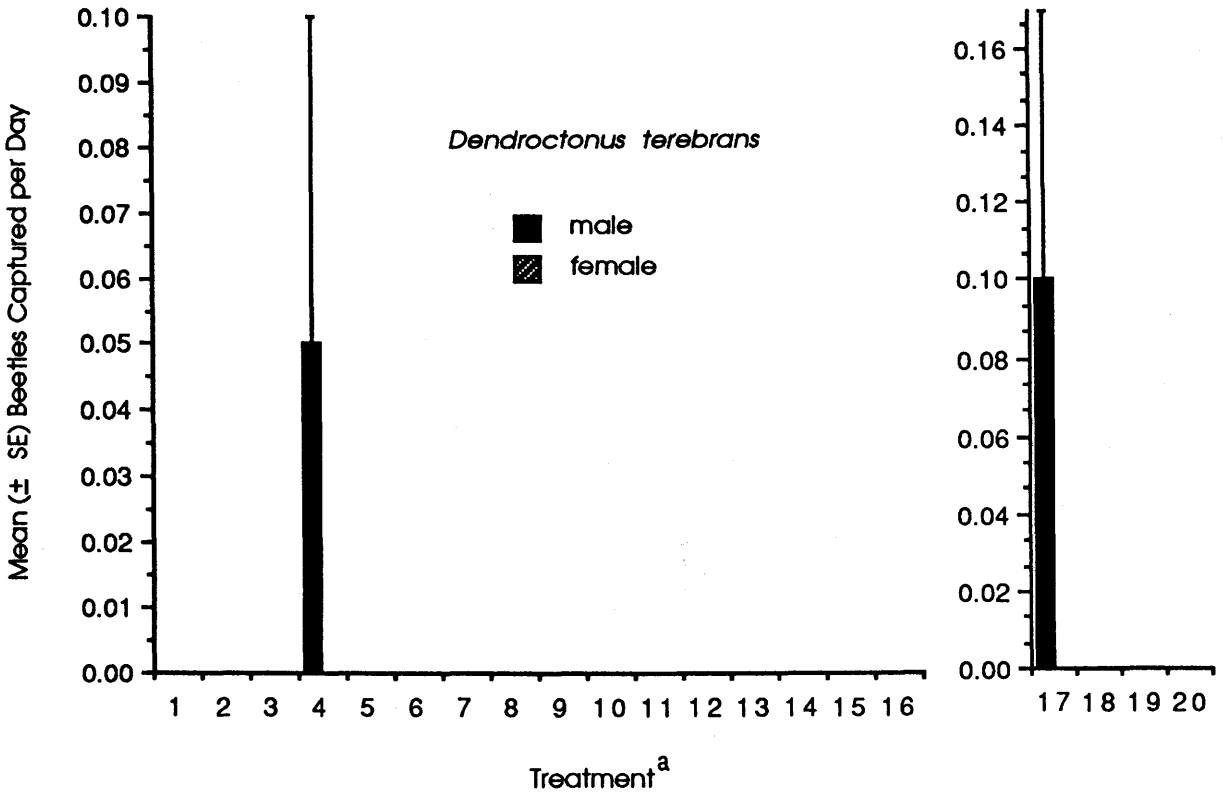

Figure 9. Mean number of *Dendroctonus terebrans* trapped in response to pheromonal compounds eluted at varying rates. [a]See Figure 8.

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attraction of *I. calligraphus* to frontalin, *trans*-verbenol, *endo*-brevicomin, *exo*-brevicomin, verbenone, and turpentine, when tested individually or in various combinations. Further, *I. calligraphus* was reported to be unresponsive to *D. frontalis*-infested bolts (Vité et al. 1964, Birch et al. 1980, Svihra 1982). Dixon and Payne (1980), however, found that *I. calligraphus* was attracted to bolts infested with female *D. frontalis*.

I. avulsus

The pheromonal blends of male *I. calligraphus* (treatments 7-9) and male *I. avulsus* (treatments 11-13) attracted both male and female *I. avulsus* (Fig. 11). The blends of male *I. calligraphus* containing racemic ipsdienol or (R)-(-)-ipsdienol (treatments 7 and 8) attracted significantly ($P > 0.05$) more *I. avulsus* than the blend containing (S)-(+)-ipsdienol (treatment 9). Also, significantly ($P > 0.05$) more *I. avulsus* were attracted to the blend of male *I. avulsus* containing (R)-(-)-ipsdienol (treatment 12) than to the blend containing racemic ipsdienol (treatment 11). The blend of male *I. avulsus* containing (R)-(-)-ipsdienol (treatment 12) was significantly ($P > 0.05$) more attractive to female than to male *I. avulsus*. Our results are in agreement with those reported for the attraction of *I. avulsus* to racemic ipsdienol and (R)-(-)-ipsdienol plus (S)-(-)-ipsenol (Hedden et al. 1976, Vité et al. 1978). Furthermore, the results support reports of the attraction of *I. avulsus* to male *I. avulsus*--and to male *I. calligraphus*-infested bolts (Vité et al. 1964, Birch et al. 1980, Svihra et al. 1980, Svihra 1982).

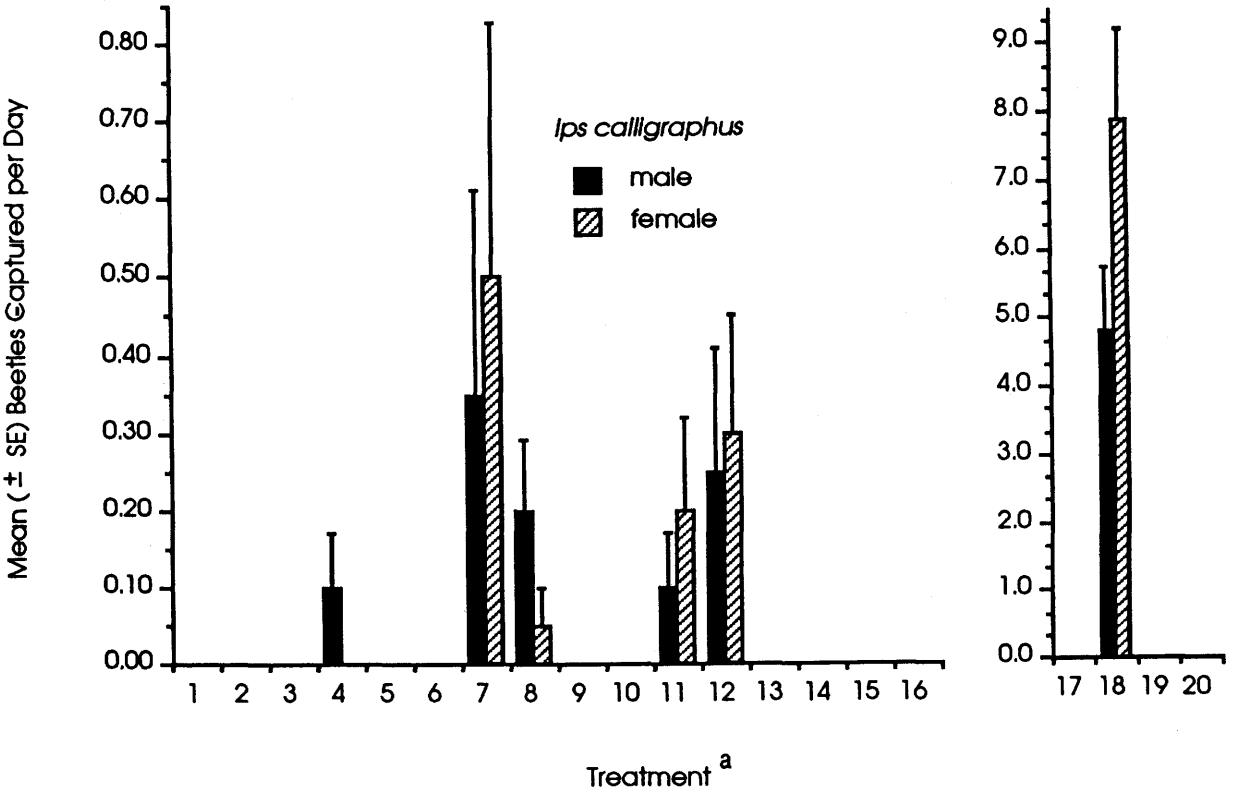

Figure 10. Mean number of *Ips calligraphus* trapped in response to pheromonal compounds eluted at varying rates. [a]See Figure 8.

Few male *I. avulsus* were attracted to the pheromone blend of male *I. grandicollis* containing racemic ipsenol; females were not attracted. The results are supported by the reported attraction of *I. avulsus* males over females to ipsenol (Hedden et al. 1976) and the attraction of *I. avulsus* to male *I. grandicollis*-infested pine bolts (Birch et al. 1980). Though not significant, *I. avulsus* also showed some attraction to the blends of female and male plus female *D. frontalis* and *D. terebrans* (treatments 1 and 3-6). While some studies have reported the lack of attraction of *I. avulsus* to *D. frontalis*-infested bolts (Birch et al. 1980, Svihra 1982), others have demonstrated attraction (Vité et al. 1964, Svihra et al. 1980). It is apparent, however, that *I. avulsus* is not strongly attracted to *Dendroctonus* pheromonal blends.

I. grandicollis

Both sexes of *I. grandicollis* were attracted to the pheromonal blend of male *I. grandicollis* containing (S)-(-)-ipsenol (treatment 15) (Fig. 12). The results support earlier reports that ipsenol (Vité and Renwick 1971b, Vité et al. 1976) and, more specifically, (S)-(-)-ipsenol (Vité et al. 1976) are attractive to *I. grandicollis*. The pheromone probably accounts in part for the attraction of *I. grandicollis* to male *I. grandicollis*-infested bolts, as reported earlier (Vité et al. 1964, Vité and Renwick 1971b, Birch and Svihra 1979, Birch et al. 1980, Svihra et al. 1980, Svihra 1982). (R)-(+)-ipsenol was not attractive by itself (treatment 16), and significantly ($P > 0.05$) reduced attraction of *I. grandicollis* to the male *I. grandicollis* blend containing (S)-(-)ipsenol (treatment 14). The results agree with previous reports that (R)-(+)-ipsenol significantly reduced the attraction of *I. grandicollis* to (S)-(-)-ipsenol (Vité et al. 1976). The blends of male *I. grandicollis* containing (S)-(-)-ipsenol attracted significantly ($P > 0.05$) more female than male *I. grandicollis* (treatment 15).

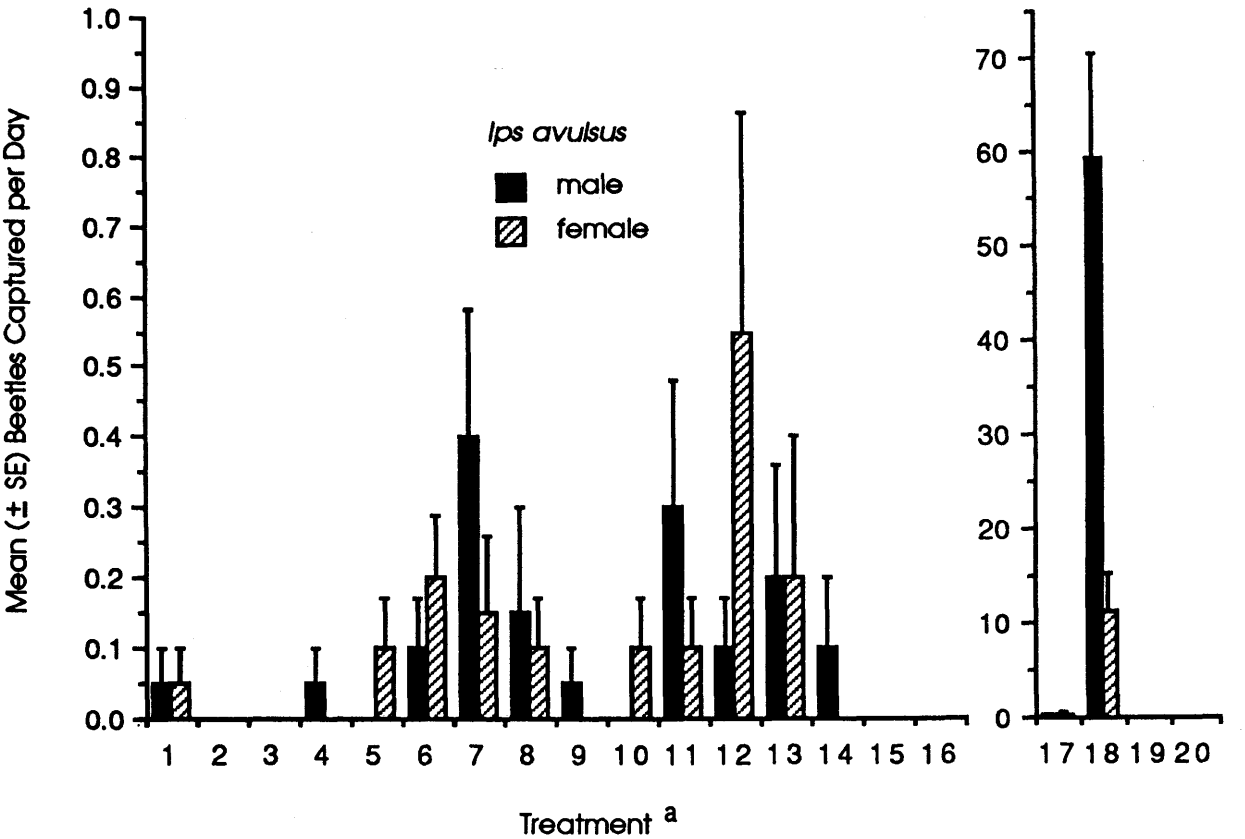

Figure 11. Mean number of *Ips avulsus* trapped in response to pheromonal compounds eluted at varying rates. [a]See Figure 8.

Most of the blends of *I. calligraphus* (treatments 7-10) and *I. avulsus* (treatments 11-13) attracted *I. grandicollis*, but at low levels. Vité et al. (1976) reported the lack of attraction of *I. grandicollis* to ipsdienol alone, which indicates the importance of the blends to interspecific communication. However, while some research has shown the attraction of *I. grandicollis* to bolts infested with *I. calligraphus* (Vité et al. 1964, Birch et al. 1980, Svihra 1982) and *I. avulsus* (Birch et al. 1980), other research has shown a lack of attraction (Vité et al. 1964, Birch et al. 1980, Svihra 1982). Without analysis of the volatiles from the bolts, of course, the blend of pheromones released in those studies cannot be determined.

The blends of male and female *D. frontalis* (treatments 1-3) and *D. terebrans* (treatments 4-6) attracted *I. grandicollis*. Significantly more ($P > 0.05$) *I. grandicollis* were attracted to a combination of male and female *D. frontalis* blends (treatment 3) than to either blend alone (treatments 1 and 2). By comparison, significantly more ($P > 0.05$) *I. grandicollis* were attracted to the blend of female *D. terebrans* (treatment 4) than to the blends of male *D. terebrans* (treatment 5) or male plus female *D. terebrans* (treatment 6). The attraction of *I. grandicollis* to the pheromonal blends of both *Dendroctonus* species supports previous reports of the attraction of *I. grandicollis* to frontalin plus *trans*-verbenol (Dixon and Payne 1980), as well as to *D. frontalis*-infested bolts (Vité et al. 1964, Birch and Svihra 1979, Birch et al. 1980, Dixon and Payne 1980, Svihra et al. 1980).

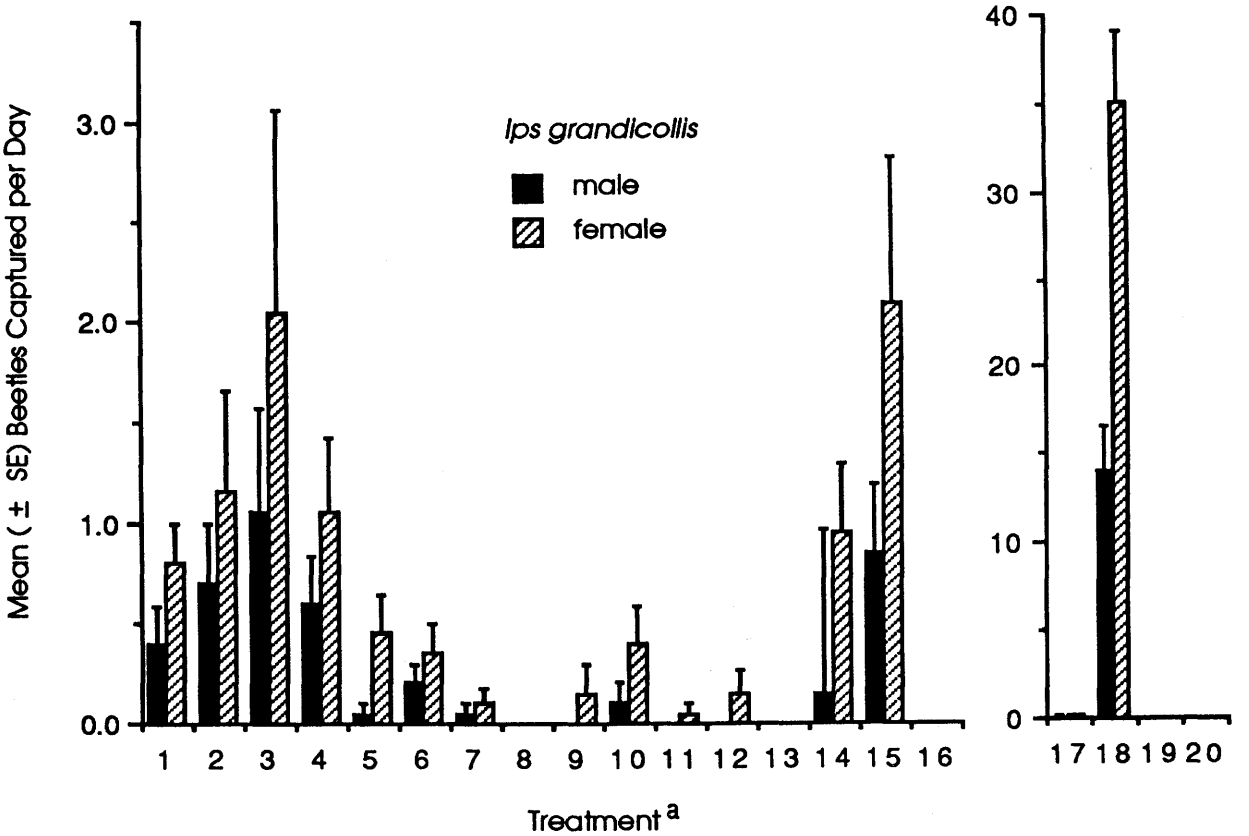

Figure 12. Mean number of *Ips grandicollis* trapped in response to pheromonal compounds eluted at varying rates. [a]See Figure 8.

As represented by turpentine alone (treatment 19), host odor did not provide an adequate stimulus to attract any of the scolytid species. It should be emphasized, however, that the release rate used was probably far less than that provided by a stressed tree in nature. In addition, the vertical silhouette alone (treatment 20), as provided by the unbaited trap, did not attract any of the five scolytid species. Thus the results verify that response by the beetles to the pheromone-baited traps was probably due to the pheromones and blends and not simply to host odor or to a visual stimulus alone.

CONCLUSIONS AND INDICATIONS

Detection of both *Ips* and *Dendroctonus* pheromonal compounds by the cohabiting species shows a sensory basis for their interspecific olfactory communication and interaction. The fact that differences in both threshold responses and relative numbers of receptors for the various behavioral chemicals do occur suggests differences in specific behavioral roles for each compound.

The field tests showed variation in behavioral response among the species in interspecific olfactory communication. *D. frontalis*, the pioneering species of the group (Birch and Svihra 1979, Birch et al. 1980, Svihra et al. 1980), apparently does not utilize *Ips* pheromones in host selection. Cross-attraction of *I. calligraphus* to male *I. avulsus*, as of *I. avulsus* to male *I. calligraphus*, was

verified. However, given our results and the mixed results of the other reports cited, the attraction of *I. calligraphus* and *I. avulsus* to *I. grandicollis* or *D. frontalis* still remains in question. *I. grandicollis* was the least specific in its responsiveness, displaying the greatest degree of cross-attraction among the cohabiting species.

Although cross-attraction ranged from none for *D. frontalis* in response to the pheromonal blends of *Ips* to extensive for *I. grandicollis*, it is probable that all five species benefit from the olfactory-based behavioral interactions. The interactions are probably most important when population levels are endemic, particularly for the less aggressive species, i.e. *I. grandicollis*, when the joint efforts of the group members are essential for overtaking the defenses of the host trees. Certainly this would increase the probability of the successful colonization of a resistant host by each species.

SUMMARY

Interspecific olfactory response was investigated in the five primary scolytid species of the southern pine bark beetle guild, *Dendroctonus frontalis* Zimmermann, *D. terebrans* (Olivier), *Ips calligraphus* (Germar), *I. avulsus* (Eichhoff), and *I. grandicollis* (Eichhoff). Antennal olfactory response was measured with the electroantennogram and single-cell techniques and showed that each species possesses receptors most sensitive to their own pheromones, but also responsive to the pheromones of the other species. Behavioral responses were measured with field trap catch data and showed that each species was attracted mostly to the pheromonal blend produced by conspecifics. Interspecifically, *D. frontalis* showed no cross-attractancy to *Ips* pheromonal blends, but was attracted to the pheromonal blend of female *D. terebrans*. All three *Ips* species showed some level of cross-attraction as well as attraction to the *Dendroctonus* pheromonal blends. Specifically, *I. calligraphus* was attracted to *I. avulsus* and slightly so to the male *D. terebrans* pheromonal blend. *I. avulsus* was more cross-attractive than *I. calligraphus* and showed attraction to the pheromonal blends of female *D. frontalis*, male and female *D. terebrans*, male *I. calligraphus*, and male *I. grandicollis*. *I. grandicollis* showed the greatest cross-attraction, particularly to the pheromonal blends of *Dendroctonus*.

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LITERATURE CITED

BILLINGS, R.F. 1985. Southern pine bark beetles and associated insects: effects of rapidly-released host volatiles on response to aggregation pheromones. Sonderdruck aus Bd. 99: 483-491.

BIRCH, M.C. and SVIHRA, P. 1979. Novel approaches to forest insect control: exploiting olfactory interactions between species of Scolytidae, p. 135-138. In Waters, W.E., ed. Current Topics in Forest Entomology. John Wiley & Sons, New York.

BIRCH, M.C., SVIHRA, P., PAINE, T.D., and MILLER, J.C. 1980. Influence of chemically-mediated behavior on host tree colonization by four cohabiting species of bark beetles. J. Chem. Ecol. 6: 395-414.

BOECKH, J. 1962. Electrophysiologische Untersuchungen an einzelnen Geruchs-Rezeptoren auf der Antennen des Totengräbers (Necrophorus, Coleoptera). Z. V.Gl. Physiol. 46: 212-248.

DICKENS, J.C. and PAYNE, T.L. 1977. Bark beetle olfaction: pheromone receptor system in *Dendroctonus frontalis*. J. Insect Physiol. 23: 481-489.

DICKENS, J.C. and PAYNE, T.L. 1978. Structure and function of the sensilla on the antennal club of the southern beetle, *Dendroctonus frontalis* (Zimmermann) (Coleoptera: Scolytidae). Insect Morph. & Embryol. 7: 251-265.

DIXON, W.N. and PAYNE, T.L. 1979. Sequence of arrival and spatial distribution of entomophagous and associate insects of southern pine beetle-infested trees. Tex. Agric. Exp. Stn. Misc. Publ. 1432. 28 p.

DIXON, W.N. and PAYNE, T.L. 1980. Attraction of entomophagous and associate insects of the southern pine beetle to beetle- and host tree-produced volatiles. J. Ga. Entomol. Soc. 15: 378-389.

FLAMM, R.O., COULSON, R.N., and PAYNE, T.L. 1988. The southern pine beetle, p. 531-553. In Berryman, A.A., ed. Dynamics of Forest Insect Populations. Plenum, New York.

GODBEE, J.F., Jr. and FRANKLIN, R.T. 1976. Attraction, attack pattern and seasonal activity of the black turpentine beetle. Ann. Entomol. Soc. Am. 69: 653-655.

HEDDEN, R., VITÉ, J.P., and MORI, K. 1976. Synergistic effect of a pheromone and a kairomone on host selection and colonization by *Ips avulsus*. Nature (Lond.) 261: 696-697.

LINDGREN, B.S. 1983. A multiple funnel trap for scolytid beetles (Coleoptera). Can. Entomol. 115: 299-302.

PAINE, T.D., BIRCH, M.C., and SVIHRA, P. 1981. Niche breadth and resource partitioning by four sympatric species of bark beetles (Coleoptera: Scolytidae). Oecologia 48: 1-6.

PAYNE, T.L. 1970. Electrophysiological investigations on response to pheromones in bark beetles. Contrib. Boyce Thompson Inst. 24: 275-282.

PAYNE, T.L. 1971. Bark beetle olfaction I. Electroantennogram responses of the southern pine beetle (Coleoptera: Scolytidae) to its aggregation pheromone frontalin. Ann. Entomol. Soc. Am. 64: 266-268.

PAYNE, T.L. 1974. Pheromone and host odor-stimulated potentials in *Dendroctonus*. Experientia (Basel) 30: 509-510.

PAYNE, T.L. 1975. Bark beetle olfaction. III. Antennal olfactory responsiveness of *Dendroctonus frontalis* Zimmermann and *D. brevicomis* LeConte (Coleoptera: Scolytidae) to aggregation pheromones and host tree terpene hydrocarbons. J. Chem. Ecol. 1: 233-242.

PAYNE, T.L. and DICKENS, J.C. 1976. Adaptation to determine receptor system specificity in insect olfactory communication. J. Insect Physiol. 22: 1569-1572.

PAYNE, T.L., COSTER, J.E., RICHERSON, J.V., EDSON, L.J., and HART, E.R. 1978. Field response of the southern pine beetle to behavioral chemicals. Environ. Entomol. 7: 578-582.

PAYNE, T.L., RICHERSON, J.V., DICKENS, J.C., WEST, J.R., MORI, K., BERISFORD, C.W., HEDDEN, R.L., VITÉ, J.P., and BLUM, M.S. 1982. Southern pine beetle: olfactory receptor and behavior discrimination of enantiomers of the attractant pheromone frontalin. J. Chem. Ecol. 8: 873-881.

PAYNE, T.L., BILLINGS, R.F., DELORME, J.D., ANDRYSZAK, N.A., BARTELS, J., FRANCKE, W., and VITÉ, J.P. 1987. Kairomonal-pheromonal system in the black turpentine beetle, *Dendroctonus terebrans* (Ol.). J. Appl. Entomol. 103: 15-22.

PAYNE, T.L., ANDRYSZAK, N.A., WIESER, H., DIXON, E.A., IBRAHIM, N., and COERS, J. 1988. Antennal olfactory and behavioral response of southern pine beetle, *Dendroctonus frontalis*, to analogs of its aggregation pheromone frontalin. J. Chem. Ecol. 14: 1217-1225.

PHILLIPS, T.W., NATION, J.L., WILKINSON, R.C., and FOLTZ, J.L. 1989. Secondary attraction and field activity of beetle-produced volatiles in *Dendroctonus terebrans*. J. Chem. Ecol. 15: 1513-1533.

RENWICK, J.A.A. 1969. Chemische Faktoren in Aggregations-Verhalten einiger Borkenkäfer. Inaug. Diss. Göttingen University.

RENWICK, J.A.A. and VITÉ, J.P. 1969. Bark beetle attractants: mechanism of colonization by *Dendroctonus frontalis*. Nature (Lond.) 224: 1222-1223.

RENWICK, J.A.A. and VITÉ, J.P. 1970. Systems of chemical communication in *Dendroctonus*. Contrib. Boyce Thompson Inst. 24: 283-292.

RENWICK, J.A.A. and VITÉ, J.P. 1972. Pheromones and host volatiles that govern aggregation of the six-spined engraver beetle, *Ips calligraphus*. J. Insect Physiol. 18: 1215-1219.

RICHERSON, J.V. and PAYNE, T.L. 1979. Effects of bark beetle inhibitors on landing and attack behavior of the southern pine beetle and beetle associates. Environ. Entomol. 8: 360-364.

SCHNEIDER, D. 1957. Elektrophysiologische Untersuchungen von Chemo-und Mechanorezeptoren der Antenne des Seidenspinners *Bombyx mori*. Z. V.Gl. Physiol. 40: 8-41.

SIEGFRIED, B.D., FATZINGER, C.W., WILKINSON, R.C., and NATION, J.L. 1986. In-flight responses of the black turpentine beetle (Coleoptera: Scolytidae) to individual monoterpenes, turpentine, and paraquat-treated slash pines. Environ. Entomol. 15: 710-714.

SMITH, M.T., BUSCH, G.R., PAYNE, T.L., and DICKENS, J.C. 1988. Antennal olfactory responsiveness of three sympatric *Ips* species [*Ips avulsus* (Eichhoff), *Ips calligraphus* (Germar), *Ips grandicollis* (Eichhoff)] to intra- and interspecific behavioral chemicals. J. Chem. Ecol. 14: 1289-1304.

SOKAL, R.R. and ROHLF, F.J. 1981. Biometry: The Principles and Practice of Statistics in Biological Research. 2nd ed. W.H. Freeman and Co., New York. 859 p.

SVIHRA, P. 1982. Influence of opposite sex on attraction produced by pioneer sex of four bark beetle species cohabiting pine in the southern United States. J. Chem. Ecol. 8: 373-378.

SVIHRA, P., PAINE, T.D., and BIRCH, M.C. 1980. Interspecific olfactory communications in southern pine beetles. Naturwiss. 67: 518-519.

VITÉ, J.P. and RENWICK, J.A.A. 1971a. Inhibition of *Dendroctonus frontalis* response to frontalin by isomers of brevicomin. Naturwiss. 58: 418-419.

VITÉ, J.P. and RENWICK, J.A.A. 1971b. Population aggregating pheromone in the bark beetle, *Ips grandicollis*. J. Insect Physiol. 17: 1699-1704.

VITÉ, J.P., GARA, R.I., and VON SCHELLER, H.D. 1964. Field observations on the response to attractants of bark beetles infesting southern pines. Contrib. Boyce Thompson Inst. 22: 461-470.

VITÉ, J.P., HEDDEN, R., and MORI, K. 1976. *Ips grandicollis*: field response to the optically pure pheromone. Naturwiss. 63: 43.

VITÉ, J.P., OHLOFF, G., and BILLINGS, R.F. 1978. Pheromonal chirality and integrity of aggregation response in southern species of the bark beetle *Ips* sp. Nature (Lond.) 272: 817-818.

VITÉ, J.P., BILLINGS, R.F., WARE, C.W., and MORI, K. 1985. Southern pine beetle: enhancement or inhibition of aggregation response mediated by enantiomers of *endo*-brevicomin. Naturwiss. 72: 99.

WAGNER, T.L., FLAMM, R.O., and COULSON, R.N. 1985. Strategies for cohabitation among the southern pine beetle species: comparisons of life-process biologies, p. 87-101. In Branham, S.J. and Thatcher, R.C. eds. Integrated Pest Management Research Symposium: The Proceedings. USDA-FS, S. For. Exp. Stn. New Orleans, Louisiana. Gen. Tech. Rep. SO-56. 383 p.

WERNER, R.A. 1972. Response of the beetle, *Ips grandicollis*, to combinations of host and insect produced attractants. J. Insect Physiol. 18: 1403-1412.